Systematics of the New Zealand short-tailed bat *Mystacina* Gray, 1843 (Chiroptera: Mystacinidae)

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Synopsis

Specimens of the short-tailed bat *Mystacina* Gray, 1843 from several localities in New Zealand show that this endemic genus consists of two species. The smaller of these, *M. tuberculata* Gray, 1843, apparently occurs throughout New Zealand, extending to at least some of the associated small islands to the south. The specimens available indicate some intraspecific variation with altitude and latitude and three subspecies are defined, two being described as new. The larger species, *M. robusta* Dwyer, 1962, found until 1965 only on two small southern offshore islands, has not been reported since and is now believed extinct. This species has not been found live on North, South or Stewart Islands since European settlement in the early part of the nineteenth century. The initial description of *M. tuberculata* and other early accounts of this species have been examined in an attempt to establish the original material seen by Gray. The early literature also shows that the other endemic New Zealand bat, *Chalinolobus tuberculatus,* should be ascribed to Gray, 1843 and not to Forster, 1844 as is customary.

Introduction

For many years the unusual endemic New Zealand genus *Mystacina* has been considered to be monospecific, its sole included species *M. tuberculata* Gray, 1843 extending throughout both North and South Islands to the small islands and islets off the extreme southern coast. Although this bat was described nearly 150 years ago, lack of suitable study material has precluded any consideration of variation within the genus until recently. Outside New Zealand it has remained known chiefly from a small number of museum specimens mostly collected during the last century, generally lacking definite locational information, and in some instances damaged. They were sufficiently adequate to establish the features of *Mystacina,* but no more.

Dwyer (1962*a*) reviewed the taxonomic history of the genus and recognised two subspecies of *Mystacina tuberculata* as he then understood it. One, smaller with proportionately longer extremities, occurring in the North Island and at least the northern areas of the South Island, he recognised as *M. t. tuberculata.* For the other, which was larger, with proportionately shorter extremities, and was found on Big South Cape Island off Stewart Island in the extreme south, he proposed the name *M. t. robusta.* Since then, Daniel (1979) and Daniel & Williams (1984) have summarised the distribution of the two supposed subspecies: *M. t. tuberculata* being found to occur on North, South and Little Barrier Islands, *M. t. robusta* found until 1965 only on two islands adjacent to Stewart Island. Daniel (1979) pointed out, however, that both forms were present in several parts of both the North and South Islands until comparatively recently, and that subfossil remains confirmed that this was so within at least the last 3000 years. Interestingly, even as recently as 1962 Dwyer disposed of no more than 11 examples in his examination of the genus. Dwyer (1962*b*) also studied wear on the upper incisors of 12 specimens of *Mystacina* in relation to the length of the skull. These he divided into two groups, one corresponding to *M. t. tuberculata,* the other to *M. t. robusta.* Apart from this, his initial studies were based entirely on external size and features, with no other detailed examination of cranial size and morphology;

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indeed, the skull of the holotype of *M. t. robusta* had to be removed from the specimen in the course of the present work.

More recently, Dwyer (1970) has examined the skulls and limb bones of *Mystacina* from various localities in both North and South Islands and from Stewart Island (see page 298), mostly of subfossil examples from limestone cave deposits. Although he found that specimens from each of the three more northerly latitudes represented by this material fell into two distinct size groups, he considered that in total his measurements did not suggest that two discrete size groups occurred, or that they indicated a north-south separation in size. Instead, he interpreted his results as indicating a continuous range from small to large in each latitudinal sample. This involved accepting a size range for *M. tuberculata* considerably in excess of that found in the majority of bat species of comparable size, but with small individuals lacking from the southernmost samples from Pyramid Valley (North Canterbury), Goulds (Opihi River, South Canterbury), Whitcombe Mountains (Westland) and from Stewart Island. On this basis he rescinded his earlier separation of *M. tuberculata* into two subspecies; nor could he find morphological criteria that would permit separation at the specific level. He remarked that his measurements also suggested that a north-south cline for increasing size might occur, but that size variation was conspicuous for any particular latitude and that the variability decreased from north to south—the latter point a reflection of the absence of small specimens from the southernmost samples. Thus he found that at 30°30′S four skulls ranged from 17·8 to 25·5 mm in length, but at 47°S four others ranged from 23·0 to 23·5 mm in their greatest length. However, the measurements tabulated by Dwyer are largely consistent with the concept of two sympatric species, while Daniel (1979) found that living populations exhibited clear-cut size distinctions in different parts of New Zealand. For this reason Daniel retained the subspecific designations, and further suggested that the marked dimensional differences between the two forms might well justify their recognition as distinct species.

This study is based predominantly on four samples of *Mystacina*. One from Big South Cape Island represents the larger form recognised by Daniel (1979) and includes the holotype of *M. tuberculata robusta* Dwyer, 1962*a*; it is supplemented by a single skeletal specimen from Solomon Island, slightly to the north. The other samples represent the smaller form recognised by Daniel and are from three widely separated localities or areas: Omahuta in the extreme north at 35°10′S, 173°37′E; the upper Waimarino River, Kaimanawa Forest Park, SE. of Lake Taupo, on the volcanic plateau of North Island at 39°02′S, 175°56′E or from localities not far distant; and Codfish Island, off the northeastern coast of Stewart Island at 46°47′S, 167°38′E. The collections of the British Museum (Natural History) have also been available; apart from a few older specimens of indeterminate or uncertain locality these include examples of the smaller form from 'the islands round Stewart Island' and more explicitly from Solomon Island. These obviously were not available to Dwyer (1962*a*, 1970) when he considered the status of *robusta*. Our initial intentions were to establish if possible the relative status of *tuberculata* and *robusta*, and to quantify variation in *Mystacina* so far as we were able to do so. We soon became aware that some doubt existed as to the actual specimens seen by Gray when he initially described the genus and its type species *M. tuberculata*, and, indeed, as to the actual vehicle and date for this publication.

Specimens examined came from the collections of the National Museum (formerly the Dominion Museum), Wellington (DM); the Auckland Institute and Museum (AIM); the Otago Museum, Dunedin (OM); the British Museum (Natural History), London (BM(NH)); and from the collection maintained by M. J. Daniel (MJD). All measurements are in millimetres.

Systematic section

Genus *MYSTACINA* Gray, 1843

Mystacina Gray, 1843*a*: 296. Type species *Mystacina tuberculata* Gray, 1843.

Mystacops Lydekker, 1891: 671. Substitute proposed in the belief that *Mystacina* Gray was preoccupied by *Mystacina* (sic) Boie, 1822, a bird, (Aves), but Boie used *Mystacinus* (Neave, 1940; Dwyer, 1962*a*).

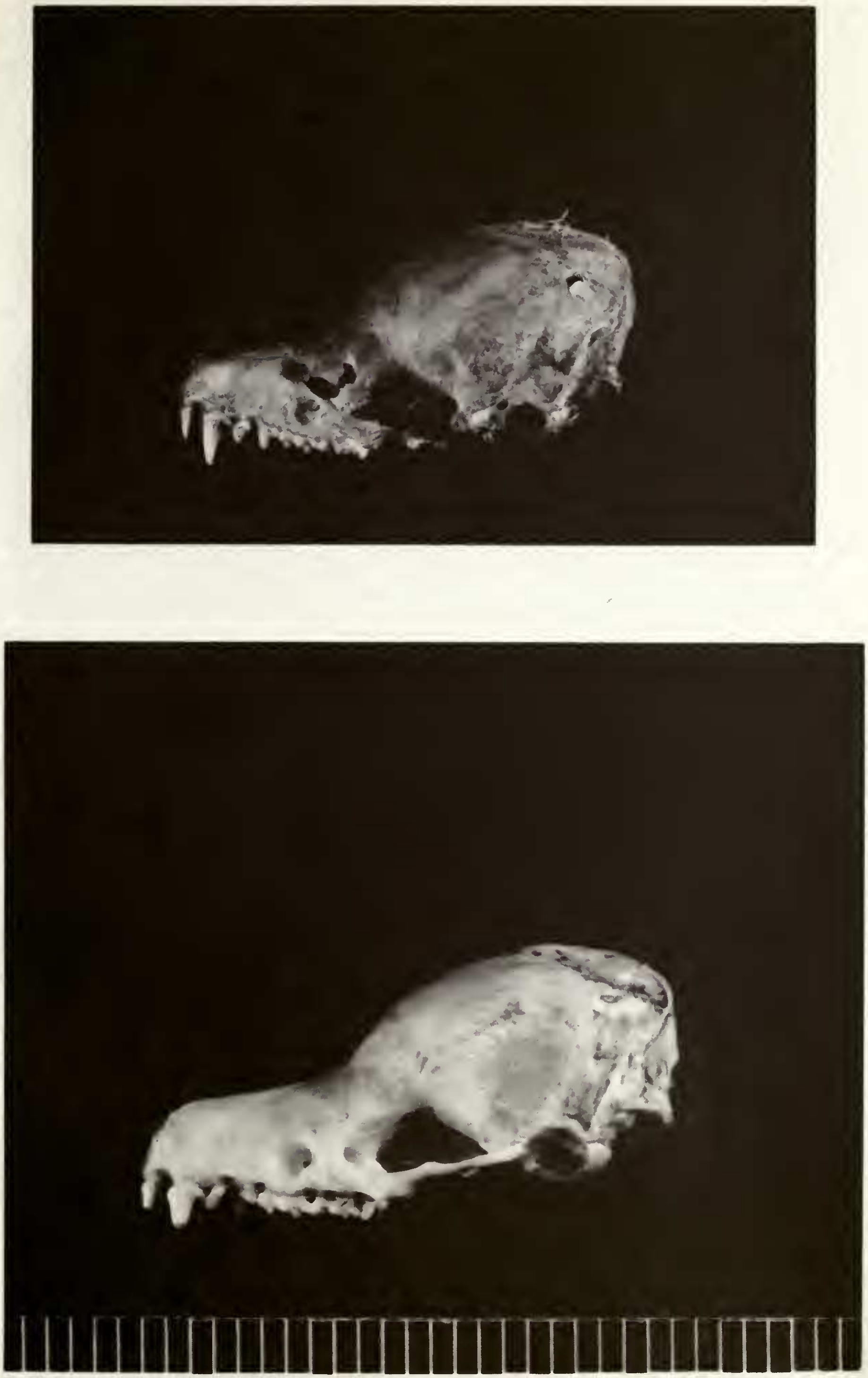

Fig. 1 Lateral view of skulls: (above) *Mystacina tuberculata tuberculata* BM(NH) 44.10.29.7, 'New Zealand'; (below) *Mystacina robusta* Holotype DM 1083, Big South Cape Island.

Dwyer (1962*a*) has provided a precise characterization of the external features of *Mystacina*. The genus may be readily recognized by its conical, obliquely truncated muzzle which has a conspicuous array of stiffened hairs radiating from the posterior margins of its glandular eminences; by its rudimentary narial pad with prominent sublateral narial openings; and by its simple ears and long, simple and attenuate tragus. The limbs are robust, the hindlimbs relatively rather short; the second digit has a single rudimentary phalanx, the third digit three bony phalanges and a cartilaginous tip, its first phalanx flexed above the metacarpal when at rest; the fifth digit is much longer than the metacarpal of the third digit, its cartilaginous tip extending slightly beyond the edge of the wing membrane. The flight membranes are thick and leathery, the propatagium reduced, the wing inserted at the ankle, with the upper surface of the plagiopatagium and the uropatagium extensively ridged near the body; the uropatagium is narrow, the short tail projecting from its upper surface.

The skull (Figs 1–7) has an elongate, rounded braincase and strong, tubular rostrum; the narial emargination is broad and deep, rounded and almost tubular; the palatal branches of the premaxillaries enclose two lateral anterior palatal foramina; the zygomata are slender, narrow and short, almost uniformly convexly curved in dorsal aspect; the anteorbital foramen is separated by a broad bar of bone, its anterior and posterior openings large, the latter occupying most of the anterior orbital wall; palate narrow anteriorly, wide posteriorly, the maxillary toothrows strongly convergent; there is a short bony post-palatal extension with U-shaped palation and the palate as a whole is slightly domed; the pterygoids are more or less parallel, the foramen rotundum large, coalesced with the optic foramen, the resulting aperture at its widest anteriorly where it is squarely truncate in outline; the audital bullae are large and well developed, their inner face unemarginated, the tympanic bullae very large, almost completely enclosing the cochleae: the basioccipital is broad, nearly as wide as one auditory bulla.

Eight palatal ridges, the anterior six undivided, the first lying between the canines, the second flexed slightly forward between the anterior premolars (pm^{2-2}); third more strongly curved forward between antero-internal corners of the second premolars (pm^{4-4}); fourth similarly curved between antero-internal corners of m^{1-1}; fifth slightly less strongly curved, joining the interspaces between m^1 and m^2; sixth straight, joining centres of internal faces of m^{2-2}; seventh and eighth shallowly divided medianly, strongly flexed, especially towards the centre of the palate, seventh originating at the interspace between m^2 and m^3, the eighth originating from the centre of the inner faces of m^{3-3}.

Dental formula i 1/1, c 1/1, pm 2/2, m 3/3 = 28. The upper incisors are large, with oblique crowns, separated basally, but in contact at about one half their height, their tips divergent, each tooth anteriorly convex, posteriorly concave, with slight lateral and posterior basal cusps; the upper canines are well developed, separated from the incisors by a narrow interspace; the upper premolars (pm^2, pm^4) are large, with pm^2 slightly the smaller, its base more or less triangular, pm^4 with distinct antero-internal cusp, the base of the tooth subsquare, both pm^2 and pm^4 with a rounded postero-internal basal cusp; the upper molars are normal, m^1 and m^2 with a long, low protocone, its commissure flexed abruptly downwards posteriorly, the inner margins of the teeth squarely truncate, each with a narrow postero-internal heel, more obviously developed in m^1; m^3 with large metacone and third commissure. The lower incisors are small but functional, compressed between the canines, deeply tricuspid and strongly expanded posteriorly, their longitudinal diameter greater than their transverse diameter; the lower canines are massive at the base and are narrowly separated posteriorly, their antero-internal margins with a distinct notch into which the outer cusp of the incisor fits; the lower premolars (pm_2, pm_4) are similar in size, pm_2 very slightly narrower than pm_4; lower molars with no especial peculiarities, m_3 with distinct entoconid and hypoconid.

The genus is endemic to New Zealand. Its two included species may be keyed:

Smaller, length of forearm 40·0–45·0 mm, condylobasal length 17·3–19·1 mm, canine to third molar (c–m^3) 7·3–8·0 mm, ears relatively long, extending to or beyond tip of muzzle when laid forward . . . . ***M. tuberculata***

Larger, length of forearm 45·3–47·5 mm, condylobasal length 21·0–22·5 mm, canine to third molar (c–m^3) 8·9–9·4 mm, ears relatively shorter, not reaching to tip of muzzle when laid forward . . ***M. robusta***

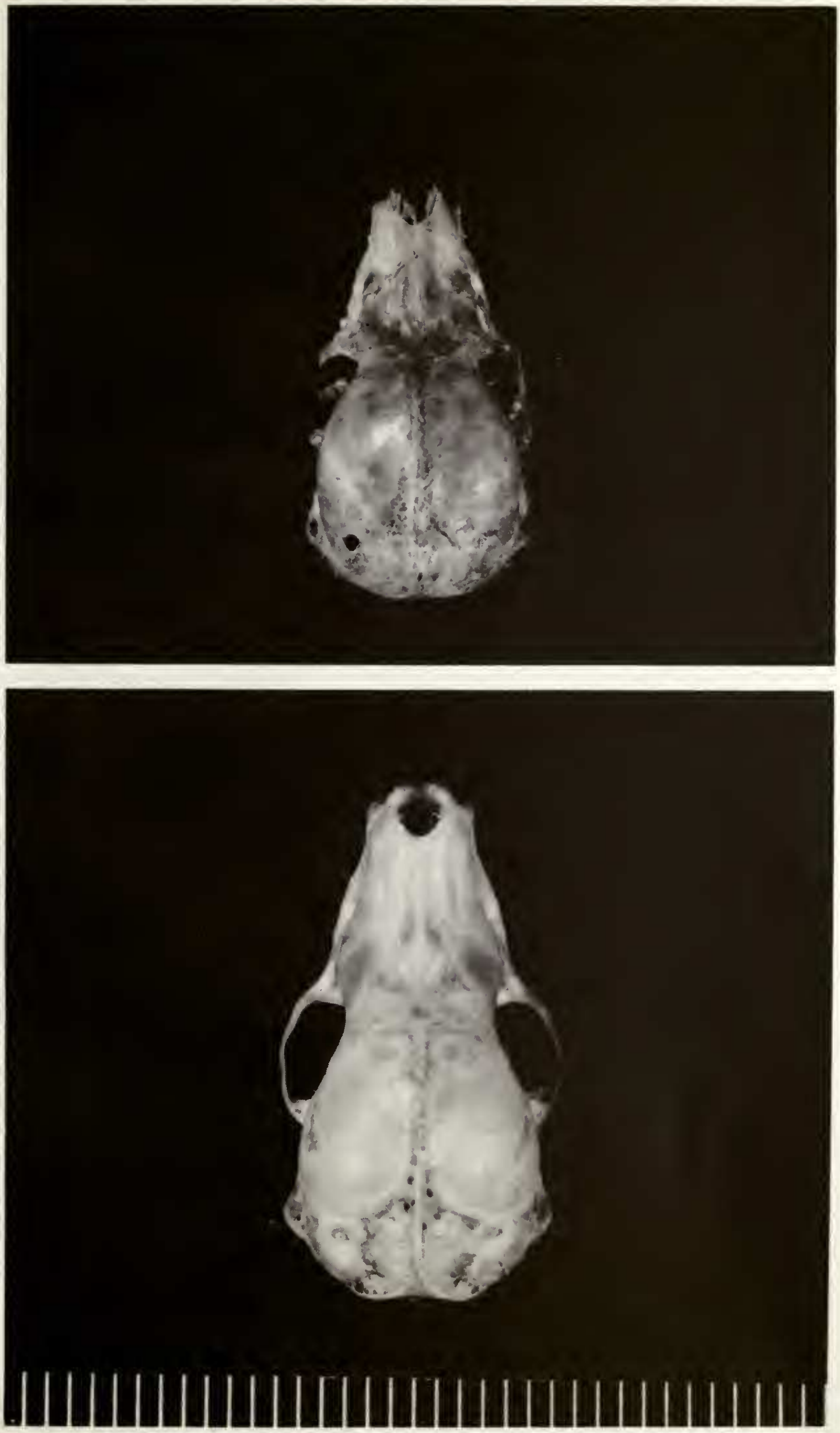

Fig. 2 Dorsal view of skulls: (above) *Mystacina tuberculata tuberculata* BM(NH) 44.10.29.7, 'New Zealand'; (below) *Mystacina robusta* Holotype DM 1083, Big South Cape Island.

Mystacina tuberculata Gray, 1843

Mystacina tuberculata Gray, 1843*a*: 296. 'New Zealand'.
Mystacina velutina Hutton, 1871: 185. Substitute: proposed to avoid the two species of bat known to be native to New Zealand sharing the same specific epithet.

ORIGINAL DESCRIPTION. The original account of *Mystacina tuberculata* has been variously cited. Tomes (1857), who may be properly regarded as first reviser, gave as its initial reference Gray's *List of the specimens of Mammalia in the collections of the British Museum*, p. 34, 1843. He added 'Gray in Dieffenb. Journ. App. p. 296, 1843'; 'Gray, Zool. Voy. Sulphur. No. II, p. 23, 1843' and 'Zool. Voy. Erebus and Terror, No. IV, pl. 22, 1844'. The names *Mystacina* and *Mystacina tuberculata* have since been attributed to one or another of these sources.

Dieffenbach, E. *Travels in New Zealand: with contributions to the geography, geology, botany and natural history of that country*. Both volumes are dated 1843; according to Sherborn (1922: xliv, cxxxiv) this work was published in January of that year. Gray (vol. 2, p. 296) properly diagnoses and describes *Mystacina tuberculata*, but in the belief that this was the bat illustrated and described, but not then published, by Forster.

Gray, J. E. *List of the specimens of Mammalia in the collections of the British Museum*. This work is dated 1843: Gray has suffixed his introductory remarks 'May-Day, 1843', and it must be presumed that it appeared after that date. Moreover the mention of *Mystacina tuberculata* (p. 34) lacks descriptive matter and the name is thus a nomen nudum in this instance.

Gray, J. E. *The Zoology of the Voyage of H.M.S. Sulphur under the command of Captain Sir Edward Belcher, R.N., C.B., F.R.G.S., etc*. This book is clearly dated 1844 and this date is attributed to it in the Catalogue of the Library of the British Museum (Natural History). Its erroneous dating of 1843 by some authors (i.e. Dobson, 1878; Honacki *et al*., 1982) appears to be through confusion with the actual narrative of the voyage by Belcher, in two volumes (Belcher, E., *Narrative of a voyage round the world, performed in H.M.S. Sulphur, during ... 1836–1842, etc*.) which is dated 1843 but which contains no mention of *Mystacina*. Moreover this account shows that H.M.S. *Sulphur* did not visit New Zealand.

Gray, J. E. *The Zoology of the Voyage of H.M.S. Erebus & Terror under the command of Captain Sir James Clark Ross, R.N., F.R.S., during the years 1839–1843*. This work evidently appeared in a number of parts. The section on Mammalia by J. E. Gray consists of three separate articles each clearly dated on the title page, the work as a whole being dated 1844–1875. The three parts on Mammalia are: *I. The seals of the Southern Hemisphere* (pp. 1–8), 1844, (pp. 9–12), 1875; *II. Miscellanea*, (pp. 12a–12d), 1875; and *III. On the Cetaceous Animals* (pp. 13–53), 1846. The account of *Mystacina tuberculata* appears in the *Miscellanea*, p. 12b. No dates are given for the plates. The British Museum (Natural History) copy of this work has a manuscript note on the first page of the *Miscellanea* article which reads 'Plates prepared in 1845, & seen privately by Krefft and other quoters, but only published, with the text, in 1875'.

It is clear, therefore, that *Mystacina* and *Mystacina tuberculata* must be cited from Gray, 1843, *in* Dieffenbach, vol. 2, p. 296, as Thomas (1905) recognized when accepting this work as the prior account, although rejecting *Mystacina tuberculata* Gray, 1843 in favour of *Mystacops velutinus* (Hutton, 1871) on other grounds.

THE TWO NATIVE NEW ZEALAND BATS. There has in the past been nomenclatorial confusion between the two native species of bat known to inhabit New Zealand, namely *Mystacina tuberculata* Gray, 1843, and *Chalinolobus tuberculatus*, usually attributed to Forster, 1844. This confusion stems from Gray, who believed the specimens that he described in 1843 (*in* Dieffenbach, p. 296) in fact represented the species seen and illustrated by Forster many years before, but whose illustration was not published until 1844. In fact, Gray on an earlier page of Dieffenbach's Travels (vol. 2, p. 181) applied the name *Vespertilio tuberculatus* to Forster's then unpublished material. The matter was resolved by Tomes (1857) who for the first time formally recognised that two species were involved, which he called *Scotophilus tuberculatus* Forster, 1844 (= *Chalinolobus tuberculatus*), and *Mystacina tuberculata* Gray, 1843. These are essentially the usages of the present day.

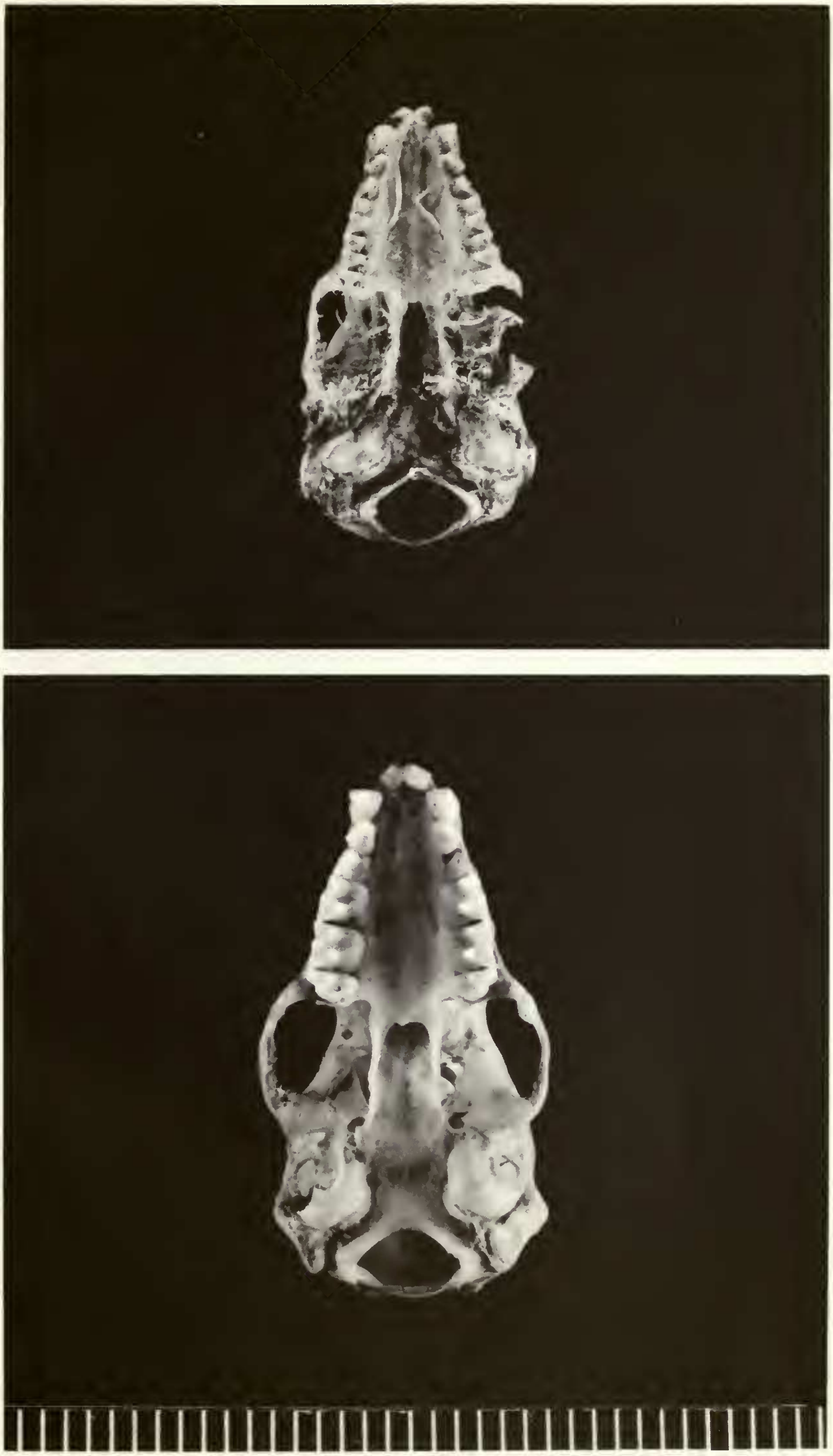

Fig. 3 Ventral view of skulls: (above) *Mystacina tuberculata tuberculata* BM(NH) 44.10.29.7, 'New Zealand'; (below) *Mystacina robusta* Holotype DM 1083, Big South Cape Island.

The first usage of *Vespertilio tuberculatus,* however, is not by Forster in 1844, but by Gray on p. 181 of volume 2 of Dieffenbach's Travels, wherein Gray provides a list of the Mammalia hitherto recorded as found in New Zealand. Under the heading Vespertilionidae he gives the entry:

1. *Vespertilio tuberculatus.* G. Forster. Icon. ined., n. 1.
Yellowish brown; ears small, rounded.
Inhab. Dusky Bay, New Zealand. G. Forster.

He remarks: 'I am not aware that any of these animals [i.e. bats] have reached Europe; they would be interesting, and doubtless new.' He also records Dieffenbach's opinion that in New Zealand . . . 'There is, apparently, only one species; probably the one figured by Forster.' Thus *Vespertilio tuberculatus* Gray, 1843 is based on the then unpublished drawing by Forster, which did not appear until the following year. As Thomas (1905) pointed out, Gray's usage of the name must take precedence and the name *Chalinolobus tuberculatus* must be ascribed to Gray, 1843, *in* Dieffenbach, vol. 2, p. 181.

Subsequently Gray, *in* Dieffenbach, vol. 2, p. 296 under the heading *'Vespertilio tuberculatus,* p. 181', stated that he had just received two specimens of this bat which he recognised as a new genus. He provided a brief description and says 'It may be called *Mystacina tuberculata'.* Thus, although under the impression that this was the bat first discovered by Forster, Gray provided the initial account of the short-tailed bat. This situation was first discussed by Thomas (1905), who recognised that the five words of description by Gray on p. 181 of Dieffenbach's second volume were sufficient to establish *Vespertilio tuberculatus* in the authorship of Gray. Thomas, however, considered that Gray's later use of *tuberculata* in combination with *Mystacina* on p. 296 of the same work (in the belief that his newly obtained specimens represented the same species) was invalidated by his previous action. As a result, Thomas employed the substitute name *velutina,* first proposed by Hutton (1871) to avoid the two native New Zealand bats sharing the same specific name. This concept has not gained general acceptance and the short-tailed bat has been known for many years as *Mystacina tuberculata.* Moreover, the International Code of Zoological Nomenclature appears to provide no support for Thomas' contention. The taxonomic history of *Mystacina* and its substitute *Mystacops* is summarized by Dwyer (1962*a*).

ORIGINAL MATERIAL. Gray stated (1843*a*: 296) that he had received two specimens of *Mystacina tuberculata,* and in his List of Mammalia in the collections of the British Museum (1843*b*: 34) he specifies two examples 'a' and 'b'. Dobson (1878), in listing the holdings of the British Museum at that date, records four specimens that apparently originate from the decade 1840–1849:

a.	ad. sk.	(type)	New Zealand.	
		(Figured in the 'Voyage of the Erebus and Terror.')		
b.	ad. sk.		New Zealand	Sir E. Belcher
c.	ad. sk.		New Zealand	Sir G. Grey [C.]
g.	skeleton	(imperfect)		

Oldfield Thomas has annotated specimen 'a' in a copy of Dobson's Catalogue in the library of the British Museum (Natural History) with the superscription 'Dr. F. J. Knox (P.)—see Trans. N.Z. Inst. IV, p. 186, 1871' and has added 'F. J. Knox (P.)' to specimen 'g'. Nothing can now found of any specimen from Belcher and there is no example of *Mystacina* recorded in the accession registers under this donor.

The remaining specimens listed by Dobson can be shown to be of a later date. They are:

d.	♀ ad., al.	New Zealand	Capt. Stokes [P.]
e,f.	ad. sks., in al.	Wellington, New Zealand	Colonial Museum [P.].

The specimen from Captain Stokes is one of three accessed in 1853 (BM(NH) 53.2.14.1–3) but none can now be found. Those from the Colonial (=National) Museum, Wellington, date apparently from 1876 but the accession register records that only a single specimen (BM(NH) 76.4.8.1) was formally entered into the collections.

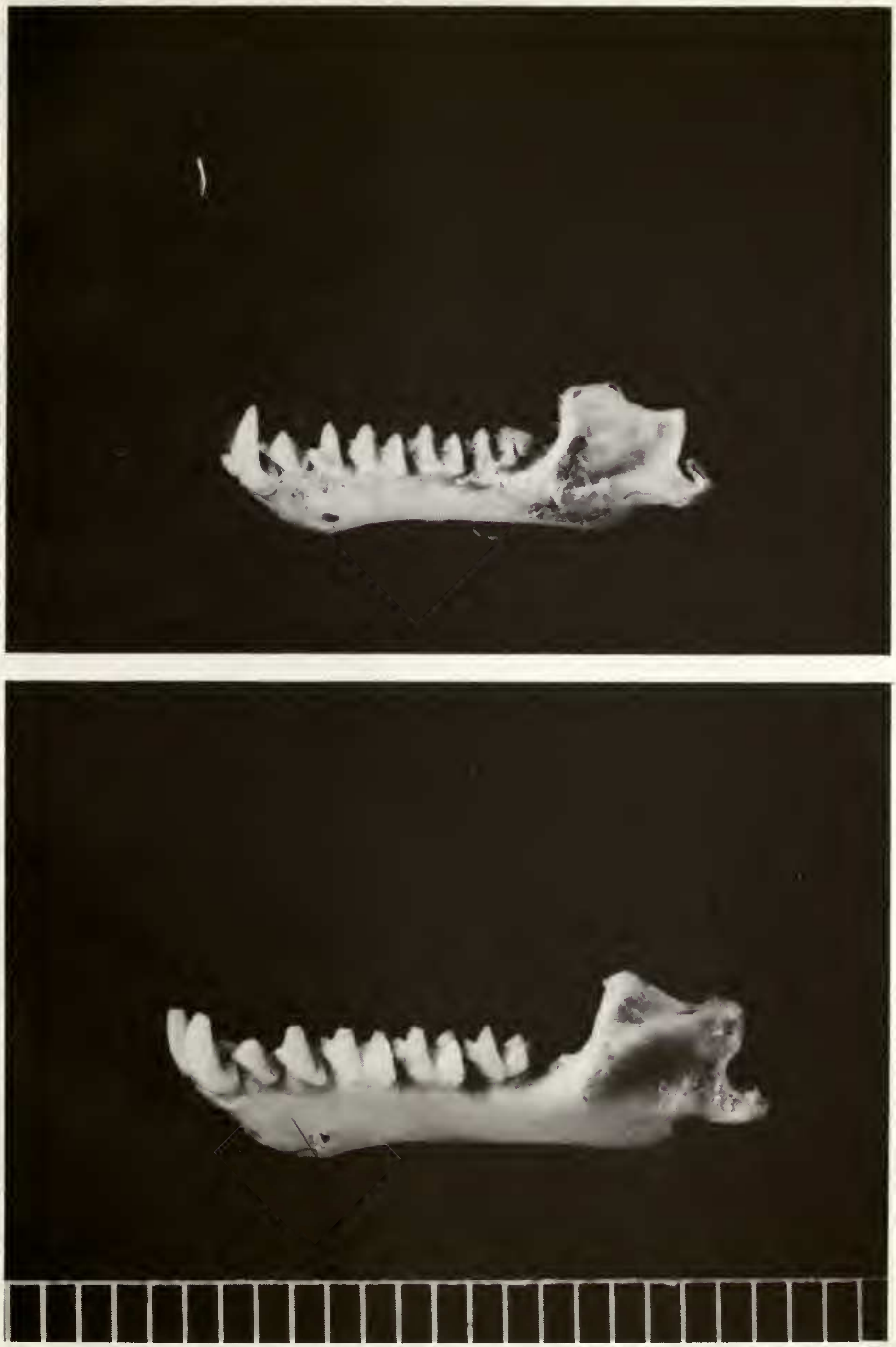

Fig. 4 Lateral view of mandibles: (above) *Mystacina tuberculata tuberculata* BM(NH) 44.10.29.7, 'New Zealand'; (below) *Mystacina robusta* Holotype DM 1083, Big South Cape Island.

There are now four specimens of *Mystacina* from the decade 1840–1849 in the collections in London, with a further example that may date from this period. They are:

> BM(NH) 42.2.8.10. New Zealand. Sir G. Grey. This is specimen 'c' of Dobson and is so marked. It is now a skin and skull but may at one time have been a mounted example. No trace of this accession number can be found in the appropriate register.
>
> BM(NH) 44.10.29.7. New Zealand. This adult skin and skull, which likewise has evidently once been a mounted specimen, bears a label in the hand of R. F. Tomes 'Fm. Brit. Mus. Coll. Feb. 1857. Lab. 44.10.29.7. Skull fig. by Ford. 117B'. The skin also has a more modern label that carries no indication of the origin of the specimen, but a similarly more modern label on the skull indicates that the specimen came from Dr Knox. The accession register has entries 44.10.29.6 and 44.10.29.7 but these are bracketed together and are suffixed 'No. 7'. According to the register this material was presented by Dr Fred Knox of Port Nicholson, New Zealand. The more modern label on the skin notes that the specimen returned to the British Museum in the Tomes Collection in 1905.
>
> BM(NH) 44.10.29.16. Part skeleton. This is specimen 'g' of Dobson. The register entry shows this also to have come from Knox and is cross referenced 'see 44.10.29.6' and 'Stuffed specimen in Coll^{n}'. Knox (1871) stated that in July, 1843 he had sent the skeleton, skin and other parts of an example of *Mystacina* to the British Museum and the inference must be that 44.10.29.6–7 and 44.10.29.16 are the accession numbers of this material.
>
> BM(NH) 49.3.2.1. New Zealand. Sir G. Grey. A skin and skull, marked 'c*' and so added in manuscript to Dobson's Catalogue by Thomas.
>
> BM(NH) 7.1.1.623. This young adult skin and skull, which again shows signs of having once been mounted, is from the Tomes Collection, received at the British Museum in 1905. The skin has been labelled by R. F. Tomes 'Fm. British Museum Jan. 1856. New Zealand. 117a'. More recent additions give the accession number and record its onetime presence in the Tomes Collection, the skull having similar more modern labels. Obviously this specimen was in the British Museum before 1856, but beyond this nothing certain can be established of its history. The register entry 44.10.29.6 carries the annotation 'Specimen with Mr Tomes 1856', perhaps suggesting that Knox might have sent two examples, one given to Tomes by Gray in 1856, the other, 44.10.29.7, given to him in 1857. However, it is now impossible to determine whether the entries 44.10.29.6–7 and 44.10.29.16 all refer to parts of a single specimen or to two specimens. Both 44.10.29.7 and 7.1.1.623 appear to have remained in the Tomes Collection for almost 50 years, and if specimen 'a' of Dobson is in fact 44.10.29.7 from Knox as Thomas thought it was, then Dobson must have recorded it while it was absent from the collections of the British Museum.

It is also interesting that the accession records of the collection presented by Dr Knox (BM(NH) 44.10.29.6–16) include a fourth entry for a bat, 44.10.29.8, which Gray has recorded as *Vespertilio tuberculata*, in contrast to the other three entries (44.10.29.6–7, 44.10.29.16) for which he has used *Mystacina tuberculata*. The specimen is still in the collections and is an example of *Chalinolobus tuberculatus* (Gray, 1843). This shows that when the register entry was completed by Gray, presumably in the latter part of 1844, he had by then distinguished the two native New Zealand bats one from the other, although initially he had believed the specimens that he called *Mystacina tuberculata* to represent the species illustrated by Forster but not then published. BM(NH) 44.10.29.8 appears to be specimen 'i' of Dobson (1878: 249), who considered it to be that figured and described by Gray in the *Voyage of the Erebus and Terror*, 1875. Thomas has annotated a copy of Dobson in the library of the British Museum (Natural History) to the effect that specimen 'i' is from New Zealand and from Dr Knox; Dobson has labelled it as the original of the figure and description by Gray in 1875. Thus Dr Knox was most probably the first to provide specimens of both native New Zealand bats in the same collection, perhaps as early as 1843, although it was not until Tomes (1857) published his detailed study of both species that their co-existence in New Zealand was formally recognized.

Gray did not designate a holotype for *Mystacina tuberculata*, and although it is evident that his two syntypes were at one time in the collections of the British Museum (probably 'a' and 'b' of his

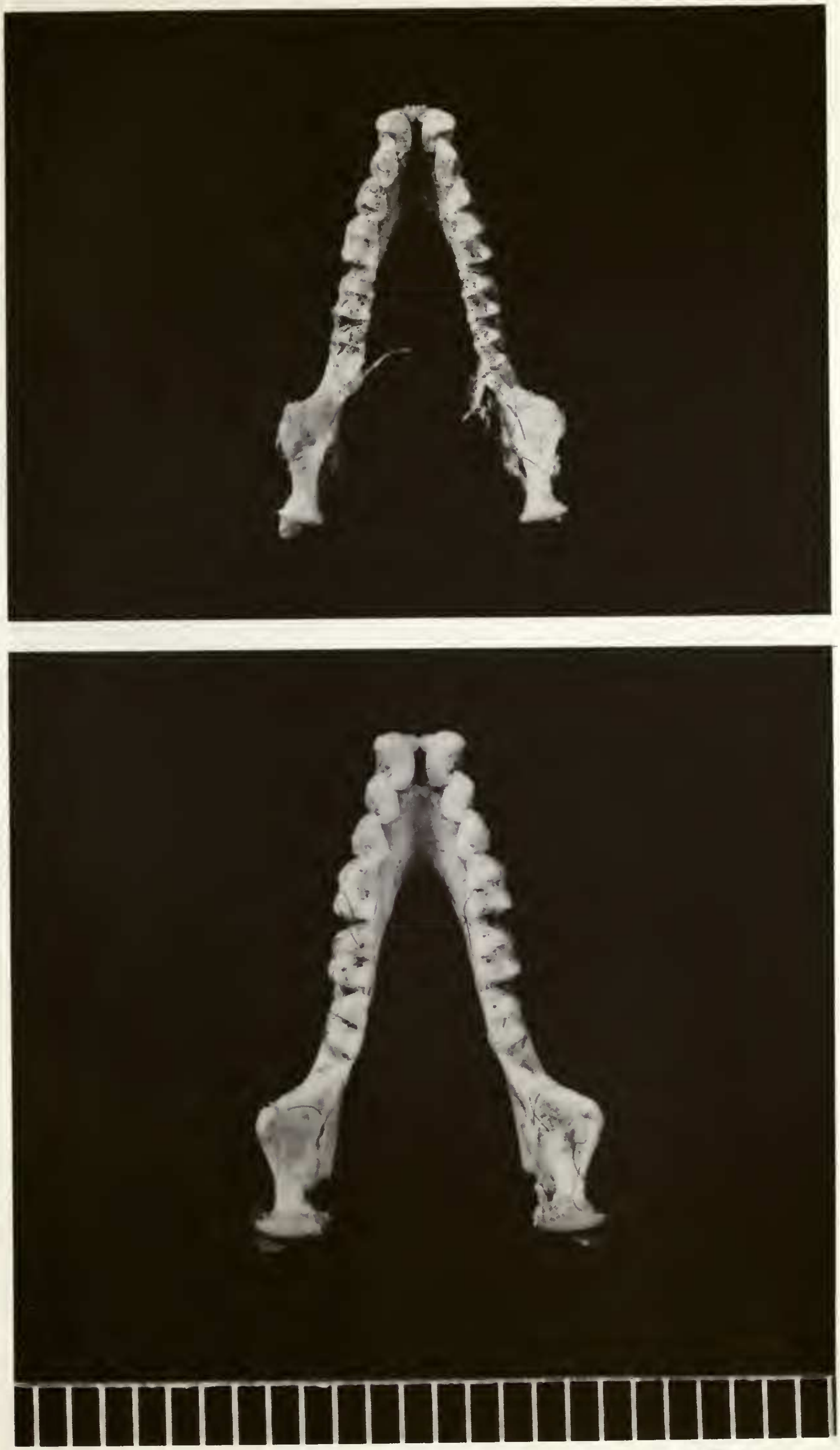

Fig. 5 Dorsal view of mandibles: (above) *Mystacina tuberculata tuberculata* BM(NH) 44.10.29.7, 'New Zealand'; (below) *Mystacina robusta* Holotype DM 1083, Big South Cape Island.

List of Mammalia, etc., 1843) there now seems no possibility of identifying either with certainty. It is even possible that they have been destroyed or have passed out of the Museum collections. Gray did provide Tomes, for instance, with the 'necessary materials' for his revision (1857), which Tomes gratefully acknowledged, at the same time keeping the specimens in his own collection. Since it is necessary to settle *tuberculata* on one or other of the two species now recognised in New Zealand, and since neither the survival nor the destruction of the syntypes can be proved, we propose that the species be interpreted by reference to one or other of the specimens from this period now in the British Museum (Natural History). Three possible candidates can be considered. Of these, BM(NH) 42.2.8.50 from Sir George Grey is young, and this collector and donor is nowhere mentioned by Gray in any of his accounts of *Mystacina tuberculata*. BM(NH) 7.1.1.623 from the Tomes Collection cannot be traced with certainty beyond 1856, and is also a young adult. The obvious choice is then BM(NH) 44.10.29.7, apparently the specimen that Dobson (1878) considered the type. This skin and skull, which was presented by Dr F. J. Knox and is therefore possibly from the environs of Port Nicholson (= Wellington), is accordingly that on which we base our interpretation of *Mystacina tuberculata* Gray, 1843. The skull is figured by Tomes (1857); if the identity with specimen 'a' of Dobson (1878) is correct, then the skin is probably the original of the plate by Gray in the *Zoology of the Voyage of the Erebus and Terror*, 1875.

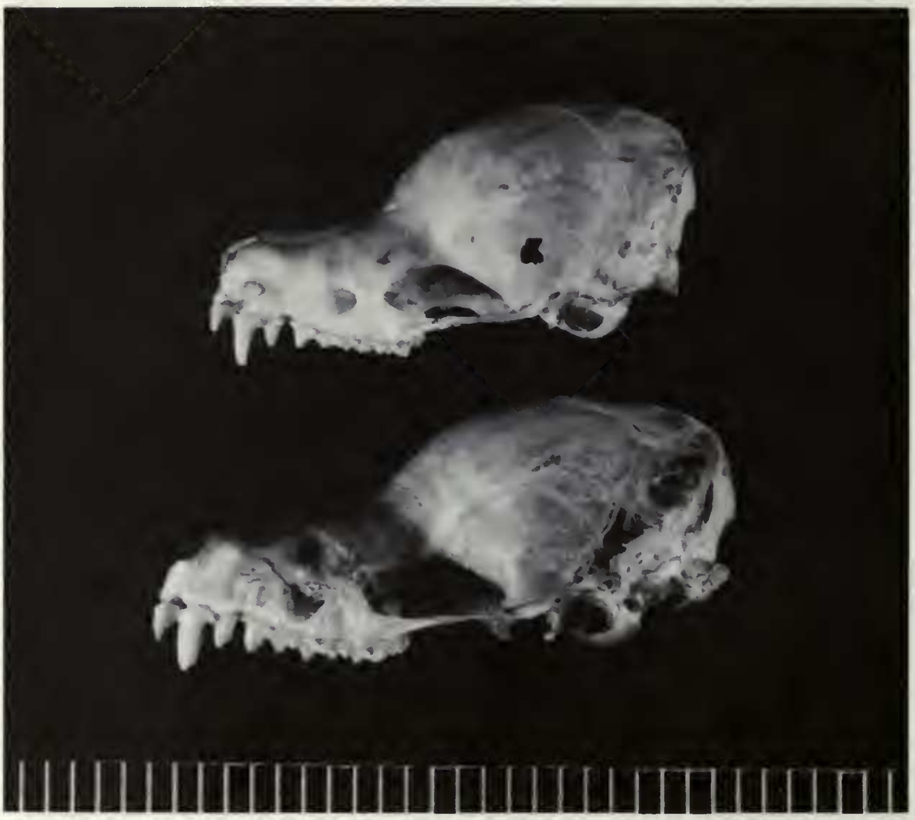

Fig. 6 Lateral view of skulls: (above) *Mystacina tuberculata tuberculata* BM(NH) 62.2116; (below) *Mystacina robusta* DM 1554, both from Solomon Island, off Stewart Island.

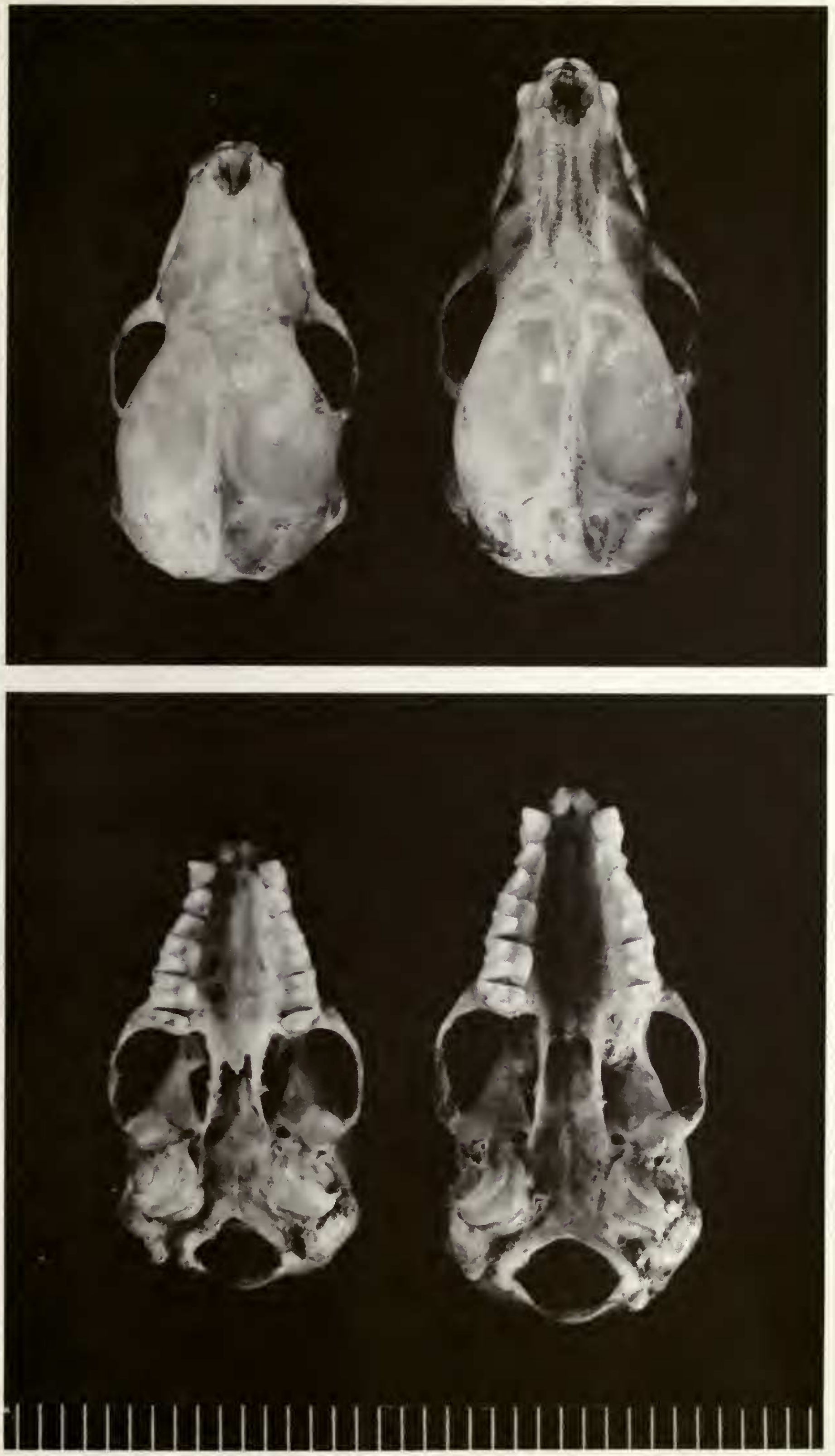

Fig. 7 Dorsal (above) and ventral (below) view of skulls: (left) *Mystacina tuberculata tuberculata* BM(NH) 62.2116; (right) *Mystacina robusta* DM 1554, both from Solomon Island, off Stewart Island.

Table 1 External measurements of *Mystacina tuberculata* and *M. robusta.*

		M. tuberculata								*M. robusta*	
		Omahuta (*M. t. aupourica*)		Waimarino, etc. (*M. t. rhyacobia*)		Codfish I., etc. (*M. t. tuberculata*)	*M. t. tuberculata* BM(NH) 44.10.29.7 'New Zealand'	*M. t. tuberculata* BM(NH) 7.1.1.623 'New Zealand'	*M. t. tuberculata* BM(NH) 76.4.8.2 Wellington			DM 1083 Holotype
Ear	6	18·5–19·1 (18·7)	10	18·2–18·7 (18·4)	14	17·4–18·9 (18·1)	—	—	17·5	8	17·7–18·6 (18·3)	18·1
Forearm	6	40·5–41·2 (40·7)	10	42·6–45·4 (44·0)	15	40·8–43·4 (42·0)	41·9	41·8	42·5	8	45·3–47·5 (46·4)	47·0
Thumb (c.u.)	6	7·1–7·9 (7·5)	10	7·8–8·6 (8·2)	14	8·0–8·9 (8·4)	7·5	7·0	7·9	8	8·9–10·3 (9·9)	10·0
Tibia	6	14·5–15·2 (14·9)	10	15·5–16·6 (16·1)	14	14·9–15·9 (15·4)	16·0	15·1	15·5	8	18·2–19·1 (18·7)	18·2
Foot (c.u.)	6	11·6–12·0 (11·9)	10	11·5–12·8 (12·1)	14	11·8–12·9 (12·2)	12·6	11·7	11·9	8	14·1–15·1 (14·6)	14·1
II^{m}	6	37·0–38·8 (37·8)	10	39·0–43·1 (41·1)	14	37·3–39·8 (38·4)	37·5	38·2	37·9	8	42·2–44·3 (43·1)	42·2
III^{m}	6	38·9–40·5 (39·7)	10	41·4–45·1 (43·3)	14	39·6–42·3 (41·2)	40·8	41·3	42·3	8	44·0–47·2 (45·7)	46·6
III^{1}	6	10·7–11·6 (11·1)	10	11·4–12·3 (11·8)	14	10·4–12·0 (11·6)	11·5	11·7	12·0	8	11·4–12·9 (12·4)	12·9
III^{2}	6	12·7–13·8 (13·2)	10	13·9–14·6 (14·2)	14	13·1–14·4 (13·7)	13·5	13·1	14·0	8	15·2–15·8 (15·4)	15·6
III^{3}	6	9·3–10·6 (10·1)	10	9·9–12·6 (11·6)	14	10·0–12·5 (11·3)	11·2	12·2	—	8	12·0–14·5 (13·2)	12·5
IV^{m}	6	38·0–39·8 (38·7)	10	41·1–44·2 (42·4)	14	38·7–41·9 (40·4)	39·8	40·0	41·1	8	42·8–45·3 (44·2)	44·8
IV^{1}	6	9·8–10·3 (10·1)	10	10·2–11·2 (10·8)	14	9·6–10·9 (10·4)	9·7	10·1	10·9	8	10·9–11·7 (11·3)	11·7
IV^{2}	6	12·4–13·3 (12·7)	10	12·7–14·0 (13·4)	14	12·1–13·4 (13·0)	13·5	12·9	13·6	8	14·6–15·1 (14·9)	14·5
V^{m}	6	35·1–36·0 (35·4)	10	36·5–40·0 (38·7)	14	35·4–38·2 (36·8)	37·2	36·4	37·8	8	39·3–42·2 (41·1)	42·2
V^{1}	6	6·1–6·7 (6·4)	10	6·6–7·2 (6·9)	14	6·0–6·8 (6·5)	6·4	6·4	7·0	8	6·4–7·8 (7·2)	7·4
V^{2}	6	10·4–11·0 (10·7)	10	11·0–11·6 (11·3)	14	9·6–11·3 (10·7)	10·7	11·1	11·6	8	11·4–12·1 (11·7)	11·7
V^{3}	6	6·5–7·2 (6·8)	10	6·4–9·1 (8·1)	14	6·0–8·5 (7·6)	—	—	8·0	8	8·0–8·6 (8·3)	8·3

Table 2 Cranial measurements of *Mystacina tuberculata* and *M. robusta*.

		M. tuberculata								*M. robusta*	
		Omahuta (*M. t. aupourica*)		Waimarino, etc. (*M. t. rhyacobia*)		Codfish I., etc. (*M. t. tuberculata*)	*M. t. tuberculata* BM(NH) 44.10.29.7 'New Zealand'	*M. t. tuberculata* BM(NH) 7.1.1.623 'New Zealand'			DM 1083 Holotype
Greatest length of skull	5	18·7–19·5 (19·0)	6	19·2–19·8 (19·5)	10	18·9–20·0 (19·4)	19·3	19·3	5	22·2–23·5 (23·2)	23·4
Condylobasal length	5	17·3–18·0 (17·9)	5	18·3–19·1 (18·8)	9	17·9–18·9 (18·3)	18·1	18·0	5	21·0–22·5 (22·0)	22·5
Condylocanine length	5	16·7–17·7 (17·3)	5	17·7–18·4 (18·1)	9	17·4–18·2 (17·7)	17·4	17·4	5	20·3–21·6 (21·2)	21·4
Basal length	5	15·3–16·2 (15·7)	5	16·1–16·9 (16·4)	8	16·1–17·0 (16·4)	16·0	16·1	5	19·0–20·1 (19·7)	20·0
Basilar length	5	14·6–15·5 (15·0)	5	15·4–16·2 (15·7)	8	15·3–16·4 (15·7)	15·4	15·6	5	18·4–19·6 (19·1)	19·4
Palatal length	5	8·4–8·9 (8·6)	6	8·6–9·3 (8·9)	10	8·5–9·4 (8·8)	8·5	9·0	5	10·4–11·1 (10·8)	11·1
Palatilar length	5	7·7–8·2 (7·9)	6	7·9–8·6 (8·2)	10	7·7–8·6 (8·2)	7·7	8·3	5	9·8–10·5 (10·2)	10·4
Length palation—basion	5	6·9–7·3 (7·1)	5	7·3–7·8 (7·5)	8	7·3–8·0 (7·6)	7·7	7·3	5	8·6–9·2 (8·9)	9·0
Width across anteorbital foramina	5	4·8–5·2 (5·0)	6	5·0–5·6 (5·3)	10	5·0–5·3 (5·1)	5·1	4·8	5	5·3–5·7 (5·5)	5·7
Least interorbital width	5	5·1–5·5 (5·2)	6	5·4–5·7 (5·5)	10	5·3–5·9 (5·6)	5·4	5·7	5	6·3–6·8 (6·6)	6·6
Zygomatic width	5	10·2–10·8 (10·4)	2	11·0, 11·1	8	10·6–11·4 (11·0)	—	—	5	11·8–12·7 (12·3)	12·7
Width of braincase	5	8·6–9·2 (9·0)	6	9·0–9·4 (9·2)	10	8·8–9·7 (9·2)	8·9	9·4	3	10·5–10·9 (10·7)	10·5
Mastoid width	4	9·7–10·2 (10·0)	6	9·8–10·6 (10·2)	9	9·6–10·7 (10·1)	10·3	10·3	3	11·3–12·0 (11·7)	12·0
c^1–c^1 (crowns)	5	4·0–4·2 (4·1)	6	4·2–4·4 (4·3)	10	4·2–4·5 (4·3)	4·1	4·1	5	4·6–4·9 (4·7)	4·9
c^1–c^1 (alveoli)	5	3·9–4·1 (4·0)	6	4·0–4·3 (4·2)	10	4·1–4·4 (4·2)	4·0	3·9	5	4·4–4·7 (4·5)	4·7
m^3–m^3 (crowns)	5	6·8–7·1 (6·9)	6	7·2–7·3 (7·3)	10	7·2–7·8 (7·4)	7·1	7·3	5	8·0–8·3 (8·2)	8·3
m^3–m^3 (alveoli)	5	6·7–7·0 (6·8)	6	7·1–7·3 (7·2)	10	7·0–7·7 (7·3)	7·0	7·2	5	7·9–8·1 (8·0)	8·1
i–m^3	5	8·2–8·7 (8·4)	6	8·4–9·0 (8·7)	10	8·5–8·9 (8·7)	8·6	8·6	5	10·1–10·7 (10·4)	10·7
c–m^3	5	7·3–7·6 (7·4)	6	7·5–8·0 (7·7)	10	7·5–7·8 (7·7)	7·4	7·5	5	8·9–9·4 (9·2)	9·4
Length complete mandible from condyle	5	12·2–12·6 (12·3)	5	12·6–13·2 (12·8)	10	12·5–13·1 (12·8)	12·7	12·9	5	14·7–15·5 (15·3)	15·4
Length right ramus from condyle	5	12·4–12·9 (12·6)	6	12·8–13·6 (13·3)	10	12·9–13·7 (13·2)	13·2	13·3	5	15·4–16·0 (15·9)	15·9
c–m_3	5	7·7–7·9 (7·8)	6	8·0–8·5 (8·2)	10	7·8–8·4 (8·1)	8·1	8·2	5	9·6–10·0 (9·9)	10·0

DIAGNOSIS. A small, comparatively delicately proportioned species, as Dwyer (1962*a*) pointed out. The species is characterized externally by its relatively large ears which in length exceed 95% of the condylobasal length of the skull and by its prominent and narrow nostrils. *Mystacina tuberculata* is generally smaller than *M. robusta* (Tables 1 & 2) but apart from this there appear to be few other clear morphological features that separate the two species. The rostrum of *M. tuberculata* is not especially heavy or massive—Dwyer (1970) remarked that the smaller skulls that he had examined were proportionately broader and deeper than one larger example with weaker sagittal and occipital crests, the cranium rising more steeply from the facial region of the skull. In series there appears to be little difference in the proportions of the skull in the two species and no consistent difference in the cranial profile. As might be expected, the cranial crests of the smaller *M. tuberculata* are weaker. The difference in skull size between the two species (Table 2, Figs 1–7), however, is strongly marked and it is immediately apparent to which species any particular skull belongs.

REMARKS. Dwyer (1970) tabulates measurements of specimens (many subfossil) from various localities throughout New Zealand. His measurement 'maxillary row' is i–m^3 rather than c–m^3: in 20 examples of *M. tuberculata* measured in the course of the present study i-m^3 ranges from 8·2 to 9·0, c–m^3 from 7·3 to 8·0, and in 5 of *M. robusta* i–m^3 varies from 10·1 to 10·7, c–m^3 from 8·9 to 9·4. The skull lengths given by Dwyer correspond closely with those of skulls examined in London, as do his mandibular row measurements (the recessed lower incisors playing little part in this length which equals approximately c–m_3) and his maxillary row measurements agree closely with i–m^3 in these specimens. It seems therefore that he had included the upper incisor in this measurement.

Wear on the upper incisors of *Mystacina* has been investigated by Dwyer (1962*b*), who found that the erosion of these teeth correlated approximately with total skull length in two parallel series, one of smaller skulls which he thought were probably *M. t. tuberculata,* the other of larger skulls, which he thought were probably *M. t. robusta.* Although none of the skulls examined in this study shows the extreme erosion figured by this author for *M. tuberculata,* in general the series supports this view. In those of *M. tuberculata* the smallest from each locality have usually but not always the least worn incisors, and the largest specimens have incisors that show at least some degree of wear. A similar relationship prevails among the small series of *M. robusta* that has been examined. It is significant that a comparison of the smallest specimen (AIM M307) of *M. tuberculata* with a condylobasal length of 17·3, and one of the smaller (DM 1554) of *M. robusta* with a condylobasal length of 22·1, shows each to have incisors at a similar stage of wear. Those of DM 1554 are, however, larger and much more massive, as are all of the teeth of *M. robusta* when compared with those of *M. tuberculata.*

INTRASPECIFIC VARIATION. The specimens of *M. tuberculata* examined include examples from three populations: one from Omahuta at the extreme north of the North Island, another chiefly from Waimarino on the high volcanic plateau in the centre of the North Island, and the third from Codfish and Solomon Islands, off the southern coast of the South Island. Small but distinct differences between these groups can be distinguished and although the available material is limited these seem sufficient to justify formal recognition.

Mystacina tuberculata aupourica subsp. nov.

HOLOTYPE. ♀ AIM M309. Omahuta Kauri Sanctuary, Northland, North Island, New Zealand, 35°10′S, 175°37′E. This locality and the origins and history of the colony whence the holotype and other specimens came is documented in detail by Holloway (1976) and by Daniel (1976). Collected 22 May 1975 by M. J. Daniel. In alcohol, skull extracted.

OTHER MATERIAL. ♂♂ AIM M310–312. ♀♀ AIM M307–308 all from type locality (in alcohol, skulls of M307, M310–312 extracted).

DIAGNOSIS. Externally and cranially small (Tables 1 & 2) for the species; ears absolutely and relatively long (Tables 3 & 4); forearm and metacarpals short (Table 3); skull small, short and narrow (Table 2).

Table 3 Major external measurements of *Mystacina tuberculata* and *M. robusta* as a percentage of the condylobasal length.

	M. tuberculata						*M. t. tuberculata* BM(NH) 44.10.29.7 'New Zealand'	*M. t. tuberculata* BM(NH) 7.1.1.623 'New Zealand'	*M. robusta*	
	Omahuta (*M. t. aupourica*)		Waimarino, etc. (*M. t. rhyacobia*)		Codfish I., etc. (*M. t. tuberculata*)					
Ear	5	103·3–106·9	5	96·3–101·1	9	94·7–101·6	—	—	4	80·4–88·1
Forearm	5	218·6–234·1	5	232·8–237·7	9	224·0–235·4	232·6	233·3	4	207·2–215·7
Thumb (c.u.)	5	41·0–43·3	5	41·4–44·4	9	42·3–49·7	41·4	38·8	4	41·7–49·0
Tibia	5	80·9–84·9	5	85·1–88·0	9	81·4–86·9	88·4	83·8	4	80·9–85·7
Foot	5	64·4–69·4	5	60·8–68·4	9	61·9–70·7	69·6	65·0	4	62·7–69·0
II^{m}	5	203·8–218·0	5	213·1–230·5	9	201·1–216·3	207·2	212·2	4	186·7–200·9
III^{m}	5	215·8–227·5	5	226·2–236·1	9	216·4–229·8	225·4	229·4	4	207·1–209·5
IV^{m}	5	211·5–223·6	5	224·6–231·4	9	211·5–227·7	219·9	222·2	4	199·1–204·1
V^{m}	5	192·9–202·9	5	199·5–212·8	9	193·4–206·6	205·5	202·2	4	187·5–190·5

MEASUREMENTS OF HOLOTYPE. Length of ear 18·8; forearm 40·5; thumb (c.u.) 7·5; tibia 15·2; foot (c.u.) 12·0; II^{m} 38·2; III^{m} 39·4; III^{1} 10·7; III^{2} 13·0; III^{3} 10·5; IV^{m} 38·5; IV^{1} 9·8; IV^{2} 12·4; V^{m} 35·1; V^{1} 6·4; V^{2} 10·9; V^{3} 6·8; greatest length of skull 19·0; condylobasal length 17·9; condylocanine length 17·3; basal length 15·6; basilar length 14·8; palatal length 8·5; palatilar length 7·7; length palation—basion 7·1; width across anteorbital foramina 5·2; least interorbital width 5·1; zygomatic width 10·3; width of braincase 8·9; mastoid width 9·9; c^{1}–c^{1} (crowns) 4·0, (alveoli) 3·9; m^{3}–m^{3} (crowns) 6·8, (alveoli) 6·7; i–m^{3} 8·3; c–m^{3} 7·4; length complete mandible from condyles 12·3; length right ramus from condyle 12·5; c–m$_{3}$ 7·8.

DISTRIBUTION. So far known only from the type locality but likely to be found in suitable sites in the lowland areas of northern North Island, New Zealand, such as Waipoua kauri forest and on Little Barrier Island.

ETYMOLOGY. The subspecific name has been derived from the Maori name Aupouri or Aupori for the nothernmost peninsula of New Zealand. This has also been used as a basis for the name of the northland faunal area of New Zealand by Knox (1980) who calls this the Aupourian faunal province.

Mystacina tuberculata rhyacobia subsp. nov.

HOLOTYPE. ♀ AIM M304. Te Rimu area, upper Waimarino River, Kaimanawa Forest Park, SE of Lake Taupo, central North Island, New Zealand, 39°02′S, 175°56′E, *c.* 700 ft. Found with others in a hollow rimu tree that had been taken to the nearby sawmill at Turangi. Obtained July 1963 by G. R. S. Gerrard. In alcohol, skull extracted.

OTHER MATERIAL. ♂♂ AIM M301–303, M306, ♀♀ AIM M300, M305 all from type locality (in alcohol, skulls of M300–302, M305 extracted); ♀ MJD unnumbered Waipakihi River, Kaimanawa Forest Park, central North Island, 39°15′S, 175°48′E (in alcohol, skull extracted); ♂ DM 1432 Ruapehu, Tongariro National Park, central North Island, 39°17′S, 175°34′E (in alcohol);—MJD unnumbered Wairata, Waioeka State Forest, west of Urewera National Park, central North Island, 38°00′S, 177°17′E (in alcohol).

DIAGNOSIS. Larger externally and cranially (Tables 1 & 2) than *M. t. aupourica*; externally the largest of the species; ears relatively short (Tables 3 & 4); forearm and metacarpals long (Table 3); skull relatively large with longer, broader palate than in the northern lowland subspecies (Table 2).

MEASUREMENTS OF HOLOTYPE. Length of ear 18·5; forearm 44·2; thumb (c.u.) 8·3; tibia 16·3; foot (c.u.) 12·8;

Table 4 Length of ear, tibia and foot of *Mystacina tuberculata* and *M. robusta* as a percentage of the length of the forearm.

		M. tuberculata									*M. robusta*
		Omahuta (*M. t. aupourica*)		Waimarino, etc. (*M. t. rhyacobia*)		Codfish I., etc. (*M. t. tuberculata*)	*M. t. tuberculata* BM(NH) 44.10.29.7 'New Zealand'	*M. t. tuberculata* BM(NH) 7.1.1.623 'New Zealand'	*M. t. tuberculata* BM(NH) 76.4.8.2 Wellington		
Ear	6	45·4–47·7 (46·1)	10	40·6–43·4 (41·9)	14	41·1–45·0 (42·9)	—	—	41·2	8	38·0–40·8 (39·3)
Tibia	6	35·8–37·5 (36·7)	10	35·8–37·7 (36·7)	14	35·0–38·8 (36·6)	38·2	36·1	36·4	8	38·7–41·7 (40·3)
Foot (c.u.)	6	28·3–30·0 (29·2)	10	25·7–28·9 (27·4)	14	27·4–30·9 (29·2)	30·1	28·0	28·0	8	30·0–33·0 (31·4)

II^{m} 43·1; III^{m} 44·1; III^{1} 12·1; III^{2} 14·6; III^{3} 12·0; IV^{m} 43·2; IV^{1} 11·2; IV^{2} 13·1; V^{m} 39·8; V^{1} 6·9; V^{2} 11·0; V^{3} 8·1; greatest length of skull 19·5; condylobasal length 18·7; condylocanine length 18·1; basal length 16·4; basilar length 15·7; palatal length 8·8; palatilar length 8·1; length palation—basion 7·8; width across antorbital foramina 5·2; least interorbital width 5·4; zygomatic width ---; width of braincase 9·0; mastoid width 10·2; c^{1}–c^{1} (crowns) 4·3, (alveoli) 4·2; m^{3}–m^{3} (crowns) 7·3, (alveoli) 7·2; i–m^{3} 8·6; c–m^{3} 7·7; length complete mandible from condyles 12·8; length right ramus from condyle 13·2; c–m_{3} 8·2.

DISTRIBUTION. So far known only from the localities listed above but likely to be found elsewhere on the volcanic plateau in central North Island and in forests adjacent to it.

ETYMOLOGY. The subspecific name derives from ρυαξ, a stream of lava, and from βιοσ, manner of living, a reference to the area in which this bat has been found.

Mystacina tuberculata tuberculata Gray, 1843

Synonymy under species heading.

ORIGINAL MATERIAL. The original specimens seen by Gray are discussed above.

TYPE LOCALITY. 'New Zealand': see discussion above.

SPECIMENS EXAMINED. —yg. BM(NH) 42.2.8.50 New Zealand (skin, skull); —BM(NH) 44.10.29.7 New Zealand (skin, skull); —BM(NH) 44.10.29.16 New Zealand (part skeleton); —yg. BM(NH) 49.3.2.1 New Zealand (skin, skull); —BM(NH) 76.4.8.2 New Zealand (in alcohol); — ♂ BM(NH) 89.10.27.2–3 Islands round Stewart Island (in alcohol); —BM(NH) 7.1.1.623 New Zealand (skin, skull); ♀ DM 1629⁽¹⁾ Big South Cape Island (in alcohol); ♀♀ BM(NH) 62.2116–2117 Solomon Island (in alcohol, skulls extracted); ♂♂ AIM M320–321, ♀♀ AIM M317–319, M322 Codfish Island, 46°47′S, 167°38′E (in alcohol, skulls of M317–318, M320–322 extracted).

DIAGNOSIS. Slightly larger externally than *M. t. aupourica* but with relatively shorter ears, longer thumbs and larger skull (Tables 1–4); ears and skull similar in proportions and size to those of *M. t. rhyacobia* but forearm and metacarpals short, their relative length much as in *M. t. aupourica* (Tables 1–3); palate long and broad (Table 2).

DISTRIBUTION. Extreme south of North Island, probably including forests of Tararua Range; possibly lowlands of South Island; islands off Stewart Island (last seen 1967 on Big South Cape and Solomon Islands, still present on Codfish Island); old record from Jacky Lee Island (Stead, 1936).

REMARKS. Examination of the measurements given by Dwyer (1970) shows that the smaller specimens that he reports from Karumu and Self Respect (38·5°S), Hukanui and Dartmoor Limestone (39·5°S) and Levin and Gouland Downs (41·0°S) are referable to *Mystacina tuberculata*. Other larger specimens from Puketiti (38·5°S), Hukunui and Bushface No. 1 (39·5°S), Gouland Downs (41·0°S), Pyramid Valley, Whitcombe Mts and Goulds (43–44°S) and Stewart Island (47·0°S) clearly represent *M. robusta*. Dwyer points out himself that two size groups are represented for the first three of these latitudes. It is interesting that the smallest specimens of *M. tuberculata* examined by Dwyer are from Karamu and Self Respect Caves, the most northerly localities from which his material came. These specimens correspond closely in size with the Omahuta population (*M. t. aupourica*), the most northerly and the smallest of those examined in London. On the other hand, one from 41·0°S (Levin and Gouland Downs) corresponds more closely in size to the Turangi population (*M. t. rhyacobia*) or to the nominate subspecies. Thus although Dwyer interpreted his measurements as displaying a continuous graduation from small to large, in fact they agree with the concept of a composite of two species, with the smaller of these dividing cranially into the two size groups into which the specimens forming the basis of the present study also fall.

Mystacina robusta Dwyer, 1962

Mystacina tuberculata robusta Dwyer, 1962*a*: 3, figs A, B, D. Big South Cape Island, New Zealand.

HOLOTYPE. ♂ DM 1083. Pukeotakeo, Big South Cape Island, New Zealand. Collected 29 April 1955 by L. C. Bell. In alcohol, skull extracted.

Specimens examined. ♂♂ DM 1083 (the holotype), 1553, ♀♀ DM 1555$^{(1)}$, 1555$^{(2)}$, 1629$^{(2)}$, 1629$^{(3)}$ 1629$^{(4)}$ Big South Cape Island; ♂DM 1554 Solomon Island, just north of Big South Cape Island (all in alcohol, skulls of DM 1083, 1553, 1554, 1629$^{(3)}$ extracted); ♀ OM unnumbered Solomon Island (skull and part skeleton).

Diagnosis. A large, robust bat with relatively shorter ears (Table 3) than *Mystacina tuberculata,* wide nostrils which lie rather closer to the muzzle than in that species, relatively slightly shorter forearm and wing elements (Table 3); rostrum slightly heavier and more massive than in *M. tuberculata,* the braincase generally rising a little less abruptly from the rostrum.

Measurements of holotype. See Tables 1 & 2.

Distribution. Big South Cape Island; Solomon Island; may occur in extreme south of South Island. It is possible that *Mystacina robusta* is now extinct, a recent survey by one of us (MJD) having found no recent evidence of its presence in the roost on Big South Cape: moreover, Maori bird hunters have not reported bats either from Big South Cape or from Solomon Island since 1967. The last positive record of *M. robusta* dates from 1965. Also, it seems likely that neither *M. robusta* nor *M. tuberculata* has ever been collected on Stewart Island although both may well have once occurred there, records from this island being based on specimens that came in fact from one or other of the surrounding islets such as Big South Cape or Solomon.

Remarks. The relatively shorter ears and wing elements of *Mystacina robusta* were interpreted by Dwyer (1962*a*) as evidence that *Mystacina* complied with Bergmann's and Allen's rules. The discovery of sub-fossil material evidently of the larger form in more northerly localities led Dwyer (1970) to re-examine the point. Having in this later paper concluded that *tuberculata* and *robusta* could be separated neither specifically or subspecifically, he had perforce to accept a wide range of size variation in *M. tuberculata* as he then understood it. His sample did not include small specimens from any southern locality, so he postulated that either only individuals with small extremities (i.e. cold-adapted) occurred in the south, the northern populations displaying the full range of size variation, or that alternatively the small individuals have only relatively recently replaced large individuals in the north. However, while it is true that a larger form with relatively shorter extremities (*M. robusta*) was found until 1965 only in the extreme south of New Zealand, it is clear from the material now available that it occurred there sympatrically with the smaller *M. tuberculata,* which also occurs in suitable locations over New Zealand as a whole—formerly the larger form seems to have been equally widespread.

Daniel (1979) has suggested that the dichotomy of the *Mystacina* stock probably occurred at a period when north–south isolation was pronounced and when the rapid onset of colder conditions, more extreme in the south, resulted in the two isolated populations evolving morphologically in accordance with the rules of Bergmann and Allen. He considered further that the most likely time for this to occur was the Pliocene and the beginning of the first Pleistocene glaciation. The smaller, less cold-tolerant form might well have survived subsequent glacial peaks in the kauri, podocarp and *Nothofagus* forests of northern New Zealand. The larger, better cold-adapted form could then have been predominant, perhaps surviving in forest refugia in the South Island. During warmer interglacials the two bats may have moved northward and southward with the re-establishment of forested areas. In more recent warmer times the smaller species has become established throughout New Zealand, and the larger form was found until 1965 only on two islands southwest of Stewart Island, although until recently both occurred in several parts of both North and South Islands. The reasons for the disappearance of the larger species are discussed by Daniel & Williams (1984).

Specimens examined in the course of this study tend to support this view. Those of *M. tuberculata* range from almost the northernmost extremity of New Zealand almost to the southernmost of the associated small islands. Thosee from the most northerly location are the smallest but have the largest ears, others from the volcanic plateau of North Island are the largest, but have relatively smaller ears and longer wing elements. Those from the southernmost population are externally slightly larger than the most northerly specimens but have smaller ears and are cranially larger, like the montane specimens from the North Island. Thus it is clear that some variation has occurred in this species, although its extent is small, and perhaps indicates a relatively recent post-glacial colonisation of much of the complex of islands. On the other hand, the greater differences separating *M. tuberculata* and *M. robusta* support a much earlier dichotomy as suggested by Daniel.

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Bibliography

Boie, F. 1822. Ueber Classification, Insonderheit der europaischen Vogel. *Isis,* Jena **10:** 545–564.

Daniel, M. J. 1976. Feeding by the short-tailed bat (*Mystacina tuberculata*) on fruit and possibly nectar. *New Zealand Journal of Zoology,* Wellington **3:** 391–398, 3 figs, 3 tabs.

—— 1979. The New Zealand short-tailed bat, *Mystacina tuberculata*; a review of present knowledge. *New Zealand Journal of Zoology,* Wellington **6:** 357–370, 5 figs, 3 tabs.

—— **& Williams, G. R.** (1984). A survey of the distribution, seasonal activity and roost sites of New Zealand bats. *New Zealand Journal of Ecology,* Wellington **7:** 9–25, 11 figs, 2 tabs.

Dobson, G. E. 1876. On *Mystacina tuberculata. Proceedings of the Zoological Society of London* 486–488, 1 fig.

—— 1878. *Catalogue of the Chiroptera in the collection of the British Museum.* Trustees of British Museum, London.

Dwyer, P. D. 1962*a*. Studies on the two New Zealand bats. *Zoology Publications from Victoria University of Wellington* No. 28: 1–28, 14 figs, 4 tabs, 4 maps.

—— 1962*b*. Wear to the incisors of the New Zealand short-tailed bat. *Records of the Dominion Museum,* Wellington **4:** 77–78, 12 figs.

—— 1970. Size variation in the New Zealand short-tailed bat. *Transactions of the Royal Society of New Zealand,* Wellington **12:** 239–243, 2 tabs.

Forster, J. R. 1844. In Lichtenstein, M. H. C. *Descriptiones Animalium quae in itinere ad Maris Australes Terras per annos 1772–74 suscepto collegit observatit et delinearit J. R. Forster . . . nunc demum editae auctoritatae . . . Academiae . . . curante H. Lichtenstein.* Koeniglich-Preussische Akademie, etc., Berlin.

Gray, J. E. 1843*a*. In Dieffenbach, E. *Travels in New Zealand; with contributions to the geography, geology, botany and natural history of that country.* John Murray, London. In two volumes.

—— 1843*b*. *List of the specimens of Mammalia in the collections of the British Museum.* Trustees of British Museum, London.

—— 1844. *Mammalia. In* Hinds, R. B. (Ed.). *The Zoology of the Voyage of H.M.S. Sulphur under the command of Captain Sir Edward Belcher, R.N., C.B., F.R.G.S., etc. during the years 1836–42.* Smith, Elder & Co., London.

—— 1875. *In* Richardson, J. & Gray, J. E. (Eds). *The Zoology of the Voyage of H.M.S. Erebus & Terror under the command of Captain Sir James Clark Ross, R.N., F.R.S., during the years 1839 to 1843.* 1. *Mammalia, Birds.* II. *Miscellanea.* E. W. Janson, London.

Holloway, B. A. 1976. A new bat-fly family from New Zealand (Diptera: Mystacinobiidae). *New Zealand Journal of Zoology,* Wellington **3:** 279–301, 68 figs, 2 tabs.

Honacki, J. H., Kinman, K. E. & Koeppl, J. W. 1982. *Mammal species of the world. A taxonomic and geographic reference.* Allen Press/ Association of Systematics Collections, Lawrence, Kansas.

Hutton, F. W. 1871. On the bats of New Zealand. *Transactions and Proceedings of the New Zealand Institute,* Wellington **4:** 184–186.

Knox, F. J. 1871. Observations on the New Zealand bats. *Transactions and Proceedings of the New Zealand Institute,* Wellington **4:** 186–188.

Knox, G. A. 1980. Plate tectonics and the evolution of intertidal and shallow-water benthic biotic distribution patterns of the SW Pacific. *Palaeogeography, Palaeoclimatology, Palaeoecology,* Amsterdam **31:** 267–297, 11 figs.

Lydekker, R. 1891. *In* Flower, W. H. & Lydekker, R. *An introduction to the study of mammals living and extinct*. A. & C. Black, London.

Neave, S. A. 1940. *Nomenclator Zoologicus. A list of the names of genera and subgenera in zoology from the tenth edition of Linnaeus 1758 to the end of 1935*. **3.** Zoological Society of London.

Sherborn, C. D. 1922. *Index Animalium sive index nominum quae als A.D. MDCCLVIII generibus et speciebus animalium imposita sunt*. Trustees of British Museum, London.

Stead, E. F. 1936. Notes on the short-tailed bat (*Mystacops tuberculatus*). *Transactions of the Royal Society of New Zealand,* Dunedin **66:** 188–191.

Thomas, O. 1905. On some Australasian mammals. *Annals and Magazine of Natural History: including Zoology, Botany and Geology,* London (7), **16:** 422–428.

Tomes, R. F. 1857. On two species of bats inhabiting New Zealand. *Proceedings of the Zoological Society of London* 134–142, 2 pls.

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